Nekton Communities in Hawaiian Coastal Wetlands: The Distribution and Abundance of Introduced Fish Species

Richard Ames MacKenzie · Gregory L. Bruland

Abstract Nekton communities were sampled from 38 Hawaiian coastal wetlands from 2007 to 2009 using lift nets, seines, and throw nets in an attempt to increase our understanding of the nekton assemblages that utilize these poorly studied ecosystems. Nekton were dominated by exotic species, primarily poeciliids (*Gambusia affinis*, *Poecilia* spp.) and tilapia. These fish were present in 50–85% of wetlands sampled; densities were up to 15 times greater than native species. High densities of exotic fish were generally found in isolated wetlands with no connection to the ocean, were often the only nekton present, were positively correlated with surface water total dissolved nitrogen, and were negatively correlated with native species richness. Native species were present in wetlands with complete or partial connection to the ocean. Additional studies are needed to document exotic fish impacts on native fish and bird habitat and whether native fish communities can contribute to invasion resistance of coastal wetlands. Future wetland restoration should include exotic fish eradication, maintenance of hydrological connection to the ocean, or programs to prevent future introductions in order to create wetlands that support native-dominated nekton communities.

R. A. MacKenzie (✉)
USDA Forest Service, Pacific Southwest Research Station,
Institute of Pacific Islands Forestry,
60 Nowelo St.,
Hilo, HI 96721, USA
e-mail: rmackenzie@fs.fed.us

G. L. Bruland
Department of Natural Resources and Environmental
Management, University of Hawaii at Manoa,
1910 East-West Rd.,
Honolulu, HI 96822, USA

Introduction

Coastal wetlands on Pacific Islands provide valuable habitat for endemic fauna and flora (Erickson and Puttock 2006) that are utilized by Pacific Islanders for fiber, fuel, food, or medicine (Naylor and Drew 1998; Drew et al. 2005; Balick 2009). Unfortunately, these ecosystems and the ecological services they provide are being lost at an alarming rate (Dahl 1990; Kosaka 1990), and the remaining wetland habitat continues to be threatened by increased development, agricultural activity, and sea level rise (Scott 1993; Allen et al. 2000; Christensen et al. 2007). Invasive species are another major threat to coastal wetlands, especially as isolated island communities are vulnerable to invasion by exotic species (Elton 1958; Paulay 1994).

Efforts to conserve coastal wetlands or restore degraded ones have significantly increased in Hawaii over the past few years (Bantilan-Smith et al. 2009), especially as wetlands provide habitat for many endangered bird species (e.g., Hawaiian stilt, *Himantopus mexicanus knudseni*; Hawaiian moorhen, *Gallinula chloropus sandvicensis*; Reed et al. 1998; DesRochers et al. 2009). Unfortunately, baseline datasets on water quality, soil characteristics, flora, and fauna from coastal wetlands are entirely lacking from this region of the world, and such datasets could significantly increase the success of these wetland mitigation projects (EPA 2002). In response to this data need, we initiated a 3-year intensive monitoring program that collected baseline data from nearly 40 coastal wetlands across the five main Hawaiian Islands (Kauai, Hawaii, Maui, Molokai, Oahu) to evaluate the water quality and

habitat functions of restored, created, and semi-natural coastal wetlands. One major component of our baseline dataset included monitoring the nekton community structure.

Nekton communities are excellent environmental indicators that have been used to determine the condition of streams, lakes, and wetlands (Karr 1981; Dionne 2000; Grabarkiewicz and Davis 2008). Their value as bioindicators is related to four main factors: (1) species differ in their tolerance to environmental disturbances; (2) most nekton spend their entire life in the water and can thus provide an integrated snapshot of biological, chemical, and physical perturbations; (3) nekton are relatively easy to sample; and (4) nekton are relatively easy to identify (Karr 1981; Grabarkiewicz and Davis 2008). In coastal wetlands, nekton communities have been used effectively to monitor the extent of impacts from pollution (Seilheimer and Chow-Fraser 2007; Driver et al. 2009), impacts of hydrological alterations to habitat quality (Eberhardt 2004), or how restored wetlands function compared with natural ones (Williams and Zedler 1999; Dionne 2000; Roman et al. 2002). Ecological parameters of fish communities (i.e., nekton growth rates, production, or reproductive success) have also been used to monitor ecosystems for sublethal stress effects (Grabarkiewicz and Davis 2008; MacKenzie and Dionne 2008).

Most previous nekton monitoring projects have occurred in coastal wetlands in continental USA. To our knowledge, no previous study has monitored nekton communities across the five main Hawaiian Islands. Nekton have been sampled from individual wetlands on Oahu, Maui, and Molokai Islands, and these sites were shown to be dominated by exotic poeciliids and tilapia (Englund 2002; McGuire 2007; Nakahara 2007; Mayer et al. 2008). These results, coupled with the prevalence of exotic fish species in other Hawaiian aquatic ecosystems (Brasher et al. 2006; Capps et al. 2009; Holitzki 2010), suggested that wetlands across Hawaii were also likely to be dominated by exotic fish species. Thus, in order to increase our understanding of the distribution of nekton species in coastal wetlands across Hawaii and create a baseline dataset of these organisms, we monitored the nekton communities across the Hawaiian Islands over a 3-year period.

Materials and Methods

Study Design

Coastal wetlands were sampled across the Hawaiian Islands in two phases. The first phase involved intensively sampling a large number of wetlands over a short period of time. Baseline data, including nekton, were collected from 38 coastal wetlands that met the following criteria.

Sites were located between 0 and 100 m in elevation. This effectively excluded all mountain bogs, which comprise a significant component of Hawaii's wetland area but are considerably different in terms of structure and function from coastal lowland wetlands. Sites were also located on one of the five major Hawaiian Islands (Hawaii, Kauai, Maui, Molokai, and Oahu; Table 1 and Fig. 1). Sites also had to be available for sampling during the study period. Many coastal wetlands were located on private property for which we could not get permission to sample or on military land with restricted access. Thus, a truly random sampling of all known coastal lowland wetlands would have been impossible. Therefore, representative coastal lowland wetland sites were chosen from a pool of all known accessible coastal lowland sites across the state. Efforts were made to achieve balance among isolated, semi-open, and open sites; across freshwater, brackish, and euhaline sites; and among semi-natural, restored, and created sites. Isolated wetlands were not connected to the ocean, open wetlands were tidally inundated two times a day, and semi-open wetlands were only connected to the ocean during the highest spring tides and/or storm events. Semi-natural refers to natural wetlands that have been affected by some type of human alteration or were influenced by adjacent human populations; natural wetlands lacking human influence were difficult to locate. Due to the large sample size ($n=38$), we feel that these sites were representative of the larger population of coastal lowland wetlands on the major Hawaiian Islands. In total, 18 semi-natural, 11 restored, and 9 created wetlands were sampled over a 4-week period in 2007. Phase II involved sampling a subset of wetlands from phase I in order to increase the temporal generality of the study. Twenty coastal wetlands were selected based on accessibility and were then sampled on a quarterly basis for 2 years (2007–2009).

Water Quality

Water samples were collected from each wetland station using a 1-L grab sampler. Dissolved oxygen, temperature, salinity, and pH were then measured using a YSI™ handheld 556 data sonde (YSI, Yellow Springs, OH, USA). Fifty milliliters of unfiltered water and 50 mL of water filtered through a 0.4-μm syringe filter were collected in the field, frozen in the lab, and later analyzed for nutrients. Filtered samples were analyzed for nitrite and nitrate (ΣNO_3; USEPA 1983), ammonium (NH_4; Fishman 1993), total dissolved nitrogen (TDN; ASTM 1995), and soluble reactive phosphorous (PO_4). Unfiltered samples were analyzed for total phosphorus (TP; Patton and Kryskalla 2003). Samples for ΣNO_3, NH_4, PO_4, and TP were analyzed with an Autoanalyzer II (Pulse Instrumentation, Saskatoon, Canada). Samples for TDN were analyzed

Table 1 Water depths (±1 SE), salinity (‰), DO (mg/L), and temperature (°C) values from phase I and phase II coastal wetlands sampled across the five main Hawaiian Islands

Sites (ID)	Status	Hydro.	PI	PII	Lift net depth (cm)	Seine/throw depth (cm)	Salinity	DO	Temp.	Benthic substrate
Hawaii Island										
Aimakapa (H1)	C	I	X	X	28.2±4.2	41.5±8.5	12.7±0.1	6.9±0.6	27.6±0.6	Silt/muck
Honuapo (H2)	N	O	X	X	28.1±2.8	53.9±6.8	14.9±2.9	6.6±0.5	23.9±0.5	Silt
Kaloko (H3)	C	O	X	X	41.0±3.7	68.9±7.7	14.0±0.8	6.7±0.4	24.6±0.8	Silt/rock
Kamilo 1 (H4)	N	I	X		15.0±3.5		10.55	8.07	22.32	Silt/rock
Mohouli (H5)	N	O	X		14.0±2.0		2.34	6.36	24.67	Silt
Waipio (H6)	N	I	X	X	30.8±11.6	133.5±8.5	0.1±0.0	5.4±0.2	25.3±0.6	Muck
Kauai Island										
Hanalei (K1)	R	S	X	X	28.3±2.3	34.6±5.3	0.1±0.0	6.7±0.4	24.8±0.5	Silt
Huleia (K2)	R	O	X		20.5±1.4		0.14	5.93	28.51	Silt
Kawaiele (K3)	C	I	X	X	28.9±2.6	37.9±4.8	8.9±0.6	7±0.3	29.3±0.9	Sand
Kawaihau C (K4)	R	O	X		12.5±4.3		19.80	4.40	23.10	Silt
Kawaihau R (K5)	N	S	X		65.0±35.0		0.22	3.45	26.43	Silt
Kilauea (K6)	N	O	X				1.08	7.92	25.13	Silt
Lawai Kai (K7)	N	O	X	X	34.4±4.6	45.6±10.2	6.6±1.5	6.2±0.4	27±1	Silt
Nukolii (K8)	C	I	X	X	23.0±4.5	24.4±4.7	15.2±2.9	7.5±1.0	31.6±1.4	Sand/muck
Maui Island										
Kanaha (M1)	N	I	X	X	25.0±5.4	24.9±1.2	5.5±0.5	7.4±0.4	29.5±1.2	Silt/muck
Kealia (M2)	N	I	X	X	33.6±5.9	44.9±8.2	14.3±7.5	7.1±0.6	25.8±0.9	Silt
Keanae (M3)	N	I	X		–		0.15	8.00	25.20	Silt
Nuu (M4)	N	I	X	X	17.6±2.1		7.6±1.3	9.9±2.4	29±0.8	Silt/muck
Paukukalo (M5)	N	S	X		–		0.50	4.75	21.09	Silt/sand
Waihee (M6)	R	S	X	X	51.2±12.0		15.6±6.9	3.9±0.8	25.5±0.7	Silt
Molokai Island										
Kakahaia (Mo1)	C	S	X	X	33.7±8.0	32.9±2.3	9.7±0.5	15.9±0.8	26.9±0.6	Silt/sand
Koheo (Mo2)	R	S	X	X	14.3±1.2	22.8±2.6	61.0±18.6	7.4±2.0	28.9±1.2	Silt/sand
Sea Farms (Mo3)	C	I	X		–		31.57	4.70	21.93	Silt
Ohiapilo (Mo4)	R	I	X	X	24.3±3.3	32.7±4.1	36.9±8.1	6.3±0.7	28.5±1.2	Silt
Ualapue (Mo5)	N	O	X	X	40.0±3.0	43.5±5.0	26±0.5	16.4±9.4	26.2±0.5	Silt/rock
Oahu Island										
Bellows (O1)	N	O	X		–		1.42	8.66	27.16	Silt/Muck
Coconut Grove (O2)	N	I	X		31.0±9.0		0.70	5.97	28.16	Silt
Hamakua (O3)	R	S	X		17.8±1.3		13.78	11.78	29.98	Silt
Kaelepulu (O4)	R	O	X		–		10.17	3.06	24.88	Silt
Kawainui (O5)	N	S	X	X	37.9±4.1	37.0±9.7	0.1±0.0	6±0.6	24.7±0.6	Silt
Kii (O6)	R	I	X		21.3±0.6		2.37	9.07	25.14	Silt
MCBH Iwa Alae (O7)	C	O	X		–		1.28	9.77	23.04	Silt
MCBH Perc. (O8)	C	I	X		–		0.38	6.52	25.79	Silt
MCBH Salvage (O9)	C	I			–		43.98	5.33	29.59	Muck
Pouhala (O10)	R	S	X	X	16.8±3.1	23.5±3.5	101.7±21.1	2.9±0.6	28.4±1.1	Silt
Punamano (O11)	N	I	X	X	35.4±1.6	57.5±3.9	0.5±0.0	5.6±0.4	26.9±0.8	Silt
Waiawa (O12)	R	S	X		16.5±2.6		50.86	6.01	28.17	Silt
Waimea (O13)	N	S	X	X	40.8±4.5	103.3±17.1	3.3±1.1	5.5±0.4	26.9±0.6	Silt/rock

Wetlands are identified by site name and site ID. Average values (±1SE) represent values that were averaged over the duration of the study (n=9). Status: C created, N semi-natural, R restored. Hydro represents the hydrological connection to the ocean: I isolated, O open, S semi-open. Muck refers to sediments that are highly organic and unconsolidated.

PI phase I, PII phase II, MCBH Marine Corps Base Hawaii

Fig. 1 Map showing the location of 38 different sampling stations across the five main Hawaiian Islands and their status (semi-natural, restored, created). *Black arrows* indicate wetlands that were dominated by native species

Legend

Wetland Sites
- ● Semi-Natural
- ● Restored
- ⊙ Created
- ☐ Coastline

0   45   90   180 Km

UTM Zone 4N, NAD83
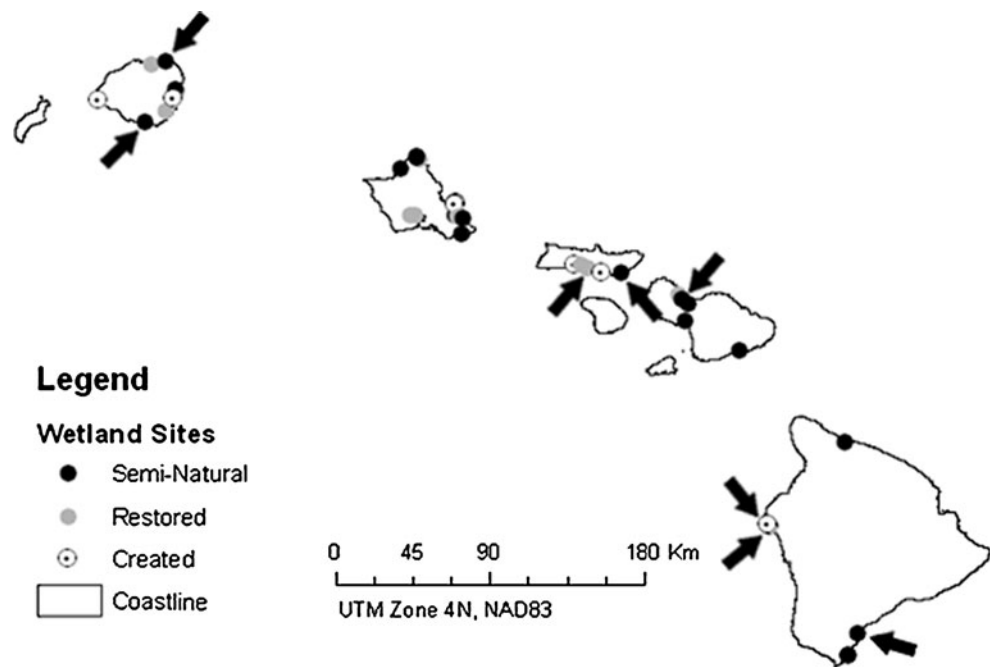
with a TOC-V/TDN analyzer (Shimadzu Instruments, Columbia, MD, USA).

Nekton Sampling

During phase I, small-bodied nekton assemblages (<100 mm total length) were sampled during the daytime from the 38 coastal wetlands on the islands of Hawaii ($n=$ 6), Kauai ($n=8$), Oahu ($n=13$), Molokai ($n=5$), and Maui ($n=6$) from March to April 2007 (Table 1 and Fig. 1). Two stations were randomly established in the shallow, open water portion of each wetland near the water–vegetation interface. A lift net (2.0 m^2, 3-mm mesh) was deployed to the left and right of each sampling station with the longest axis of the net parallel to and 1–2 m away from the water–vegetation interface. A total of four nets were deployed in each wetland. All attempts were made to sample open and semi-open sites within 1 h of the low tide turning; average water depths across most sites varied from 18 to 34 cm (25th to 75th percentile; Table 1). Benthic substrate at most sites was dominated by fine-grained sediments (e.g., silt, sand). After an acclimation period of 30–45 min, nets were lifted out of the water and all nekton were processed. Each lift net collected one sample; if no nekton were collected, a zero was recorded for that net. Fish, shrimp, and crabs were then identified, counted, measured to the nearest mm, and weighed to the nearest 0.01 g. Fish and shrimp were measured for total length (i.e., tip of rostrum to end of telson); crabs were measured for carapace width. Density estimates were calculated by dividing the total number of nekton by the area of the lift net (2.0 m^2), which were then averaged across all four lift net samples.

During phase II, small-bodied nekton assemblages were re-sampled from 20 of the phase I wetlands (Table 1) during the daytime every 3 months from September 2007 until September 2008 using the previously described lift nets. In order to increase the resolution of the nekton community structure sampled, alternative fishing gear types were used at the same open water sampling stations as the lift nets for the remainder of the project (December 2008–June 2009). Large-bodied nekton assemblages (>100 mm total length) were sampled during the daytime using a 15-m-long purse seine (10-mm mesh) and a 2-m radius throw net (6-mm mesh). A single seine sample was taken from one of the two stations at each wetland. One end of the seine net was held stationary at the vegetation–water interface, while the other end was moved away from the stationary end through the water in a circular pattern until the two ends met and formed a circle. All attempts were made to set and pull seine nets for the same duration and over the same area (18.4 m^2) at each site. Fish were processed as described above. A single throw net sample was taken at each station. If the net did not fully open, the net was re-thrown in an adjacent area. Assuming that we had sampled a perfect circle with the throw net, the area sampled was roughly equal to the area of the throw net (18.0 m^2). Like lift nets, these gear types sampled the shallow, open water areas adjacent to the vegetation–water interface. However, the greater areas sampled by these nets resulted in greater water depths sampled and sites varied from 33 to 52 cm (25th to 75th percentile). Density estimates for each gear type were then calculated by dividing the total number of nekton by the area sampled by the seine or the throw net. Total densities were then determined by summing seine and throw net densities for each species.

Statistical Analyses

Dissolved oxygen concentrations (milligrams per liter), temperature, water depth, salinity, and pH from phase I were compared among wetland type (semi-natural, restored, created) and hydrological connection to the ocean (isolated, semi-open, open) using a two-way analysis of variance (ANOVA). Fixed factors included wetland type, hydrology, and their interaction. These same parameters from phase II were also compared among wetland type and hydrological connection. However, there were not always replicate wetland types within each hydrological connection and vice versa, so comparisons were made using one-way ANOVAs that accounted for repeated measures (over time) in each wetland. Depth and salinity values did not meet assumptions of normality and equal variance and were log $(x+1)$ transformed prior to analysis. The covariance structures for all repeated measures were autoregressive of order 1 (i.e., measurements on the same wetland in December 2007 were potentially more correlated with March 2008 than June 2008). Post hoc analyses were conducted using the Tukey–Kramer method, and all ANOVAs were performed in PROC MIXED (SAS 9.1) at an alpha level of 0.05.

Community compositions of small-bodied nekton from each phase II wetland sampling event were compared across islands (Hawaii, Kauai, Maui, Molokai, Oahu), wetland types (semi-natural, restored, created), and hydrologic connection to the ocean (isolated, open, semi-open) using non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) in PRIMER 6 (Clarke 1993). A Bray–Curtis similarity matrix was first created from log$(x+1)$-transformed nekton densities. NMDS then ordinated sites based upon similarities into a two-dimensional space. Patterns of similarity and the factors responsible for those patterns were visually explored using cluster analyses set at resemblance levels of 20%, 40%, 60%, and 80% and by changing the factor levels of data points (island, wetland type, hydrology). ANOSIM was then used to statistically compare levels of similarity across islands, wetland types, and hydrology. Species responsible for those differences were identified using a similarity of percentage (SIMPER) procedure in PRIMER 6, which measures dissimilarity by making pairwise comparisons of nekton abundances among islands, wetland types, or hydrological connections. Species were then ranked in order of their percent contribution to dissimilarity.

Relationships between nekton community structures and environmental variables [salinity, depth, pH, dissolved oxygen (DO), temperature, $\sum$NO$_3$, NH$_4$, TDN, PO$_4$, TP] were examined using the BIO-ENV routine in PRIMER 6. BIO-ENV uses Spearman rank correlation to calculate dissimilarity between Bray–Curtis and Euclidian similarity

matrices created from log$(x+1)$-transformed nekton densities and square-root-transformed environmental variables, respectively. Correlations (ρ) were then made between all possible combinations of environmental variables (i.e., k variables at a time ranging from one to all variables) and nekton community structure.

Relationships between densities of exotic species, densities of native species, nutrient concentrations ($\sum$NO$_3$, NH$_4$, TDN, PO$_4$, TP), water depth, temperature, dissolved oxygen concentrations, pH, and salinity were also examined using Pearson's correlations in SYSTAT 10. Because there was a change in fishing gear, only data collected from lift nets (March 2007 through September 2008) were used. All factors except dissolved oxygen and temperature did not meet assumptions of normality. Fish densities were log$(x+1)$ transformed prior to analyses; all other factors were log transformed.

To determine whether exotic fish density declined with increased native species richness, we conducted regression analyses with one-tailed alternative hypotheses (decline) in SIGMA PLOT 11. Native species richness was used as the dependent variable versus native densities because native biodiversity can increase the resistance of an ecosystem to invasion (Mitchell and Knouft 2009; Flaspohler et al. 2010). For example, there is a greater chance that piscivorous species that can control invasive fish populations through predation will be present in more diverse ecosystems. Linear regressions were conducted on log$(x+1)$-transformed exotic fish densities and non-transformed native species richness from lift nets and from seines and throw nets. Lift net datasets included values collected from each of the wetlands that contained fish assemblages ($n=35$); data from sites sampled in both phase I and II were averaged across quarterly samples taken. Seine and throw net data from phase II were also averaged across quarterly samples.

Results

Physicochemical Parameters of Wetlands

Physicochemical parameters varied across sites in both phases I and II (Table 1) and did not significantly differ across wetland type (semi-natural, created, restored) or hydrology (open, semi-open, isolated). The only exception occurred when DO levels were compared across wetland types. DO significantly differed among wetland type in phase I ($p<0.05$, $F=3.91$, $df=2, 18$) and phase II ($p<0.001$, $F=8.36$, $df=2, 47$). In phase I, DO levels were significantly greater in created wetlands than either restored ($p<0.05$) or semi-natural ones ($p<0.05$). In phase II, DO levels were significantly greater in created ($p<0.05$) and semi-natural wetlands ($p<0.05$) than restored ones.

Water temperatures varied across wetland types in phases I and II. Average temperatures were 2–4°C warmer in isolated and semi-open wetlands compared with open wetlands in both phase I (27.7±0.7°C, 27.1±1.1°C, and 24.8±0.5°C, respectively) and phase II (29.5 ± 0.6°C, 29.3±0.9°C, and 25.8± 0.5°C, respectively). These differences were not significant, which were likely due to the large standard errors that resulted from occasional temperature extremes (>30°C) measured in isolated and semi-open wetlands.

Salinities were also variable across wetland types, but average values were generally higher in restored wetlands than the created or semi-natural ones in phase I (31.5± 14.4‰, 14.5±4.8‰, 9.3±4.3‰, respectively) and phase II (59.2±11.1‰, 13.7±1.3‰, 10.4±1.7‰, respectively). Salinities were also higher in isolated and semi-open wetlands than open wetlands in phase I (13.8±5‰, 32.5± 16.2‰, and 8.8±2.8‰, respectively) and phase II (26.4± 6‰.4, 21.5±6.7‰, and 15.2±1.8‰, respectively). These differences were not significant due to the large degree of variability among sites and hydrological connection to the ocean.

Depths also varied across wetland types, but average values were generally higher in semi-natural and created wetlands than the restored ones in phase I (29.3±11.9, 31.0± 3.0, and 21.8±4.4 cm, respectively) and phase II (32.7±3.6, 30.7±3.2, and 14.2±0.8 cm, respectively). In phase I, average depths were higher in open (27.5±2.7 cm) and isolated wetlands (26.2±3.0 cm) than in semi-open ones (24.2± 4.6 cm). In phase II, depth was higher in open (36.4±3.7 cm) and semi-open wetlands (26.0 ± 6.0 cm) than the isolated ones (23.8±3.0 cm). These differences were not significant due to the large degree of variability among sites and hydrological connection to the ocean.

Phase I Nekton Community Composition

A total of 3,214 nekton were sampled using lift nets in phase I. Total numbers of nekton and species richness were higher for exotic species (2,824 fish, 20 species) than native species (390 fish, 11 species; Table 2). Six of the native species collected were endemic (*Alpheus rapax*, *Eleotris sandwicensis*, *Kuhlia sandvicensis*, *Kuhlia xenura*, *Stenogobius hawaiiensis*, *Psilogobius mainlandi*).

Twenty-seven of the 38 wetlands sampled were dominated by exotic nekton species. High numbers of exotic nekton were due to the occurrence of mosquitofish (*Gambusia affinis*) and mollies (*Poecilia* spp.). Preliminary molecular analyses have revealed that many of the *Poecilia* spp. collected were the exotic Mexican molly, *Poecilia mexicana* (MacKenzie, unpublished data). However, they will be referred to as *Poecilia* spp. for the remainder of the paper. Other exotic fish included guppies (*Poecilia reticulata*), swordtails (*Xiphophorus helleri*), and tilapia. Only

juvenile tilapia were collected, which are difficult to identify without the aid of genetic markers and were thus identified only to tilapia. Average densities of exotic species were 15 times greater than native species densities and represented 50–90% of nekton densities sampled (Fig. 2).

Only eight wetlands had nekton densities dominated by native species. These sites included Kilauea (Kauai), Lawai Kai (Kauai), Aimakapa (Hawaii), Honuapo (Hawaii), Kaloko (Hawaii), Koheo (Molokai), Ualapue (Molokai), and Paukukalo (Maui; Fig. 1). The four most common native species included mullet (*Mugil cephalus*), flagtails (*K. sandvicensis* and *K. xenura*), and feeble shrimp (*Palaemon debilis*). Native species were generally rare from Oahu wetlands and were only collected from two sites (Pouhala and Waimea). The remaining three wetlands, Kamilo 1 (Hawaii), Nuu (Maui), and Waihee (Maui), were completed devoid of nekton.

Phase II Nekton Community Composition

A total of 12,825 nekton were sampled using lift nets from September 2007 through September 2008 from the 20 wetlands across the five islands during phase II. Total numbers of nekton were higher for exotic species (9,359 fish) than native species (3,466 fish), while species richness was higher for native species (13) than exotic species (11). The same six endemic species collected in phase I lift nets were also collected in phase II lift nets (*A. rapax*, *E. sandwicensis*, *K. sandvicensis*, *K. xenura*, *S. hawaiiensis*, *P. mainlandi*).

Lift net data from phase II revealed patterns that were similar to those observed in phase I (Fig. 3). Densities of small-bodied nekton communities in 12 of the 20 wetlands were dominated by exotic species throughout the year, which was due to the abundant mosquitofish and mollies. Native species densities were only dominant in 5 of the 20 wetlands, all of which were open or semi-open systems [Lawai Kai (Kauai), Honuapo (Hawaii), Kaloko (Hawaii), Koheo (Molokai), Ualapue (Molokai)]. Native species were represented by mullet, flagtails, and feeble shrimp; less abundant native fish included the predatory barracuda (*Sphyraena barracuda*). While native species (i.e., feeble shrimp) were originally the dominant species in the Aimakapa wetland site on Hawaii Island, densities of exotic guppies increased over the study period and resulted in that site becoming dominated by exotic fish species.

Small-bodied nekton assemblages sampled over the duration of the project with lift nets clustered into three distinct groups at the 20% similarity level and four distinct groups at the 40% similarity level at a stress value of 0.1. This stress value indicates that the patterns observed correspond to a robust ordination with minimal chance of biased interpretation (Clarke 1993). Visual examination revealed that neither island (Kauai, Hawaii, Maui, Molokai,

Table 2 List of species collected from wetlands during phase I and phase II nekton sampling events

Taxa/scientific name	Common name	Sampling site
Mollusks		
Corbicula fluminea	**Asian clam (E)**	K1, M3, O11
Pomacea canaliculata	**Apple snail (E)**	K1
Stylocheilus longicauda	Sea hare (N)	Mo2
Crustaceans		
Alpheus rapax	Hawaiian goby shrimp (End)	H2, Mo5
Brachycarpus biunguiculatus	Two claw shrimp (N)	K7, Mo5
Macrobrachium lar	**Tahitian prawn (E)**	K7, O13
Palaemon debilis	Feeble shrimp (N)	H1, H2, H3, K6, K7, M2, Mo2, Mo5, O10
Pilodius areolatus	Aereolated crab (N)	Mo5
Procambarus clarkii	**Red swamp crayfish (E)**	M2, O2, O11
Scylla serrata	**Samaoan crab (E)**	K7, Mo2
Thalamita crenata	Crenate crab (N)	Mo2, Mo5
Fishes		
Abudefduf abdominalis	Hawaiian sergeant (End)	Mo5
Acanthurus nigrofuscus	Brown surgeonfish (N)	Mo5
Arothron hispidus	White spotted puffer (N)	H2, Mo2, Mo5
Asterropteryx semipunctatus	Half-spotted goby (N)	Mo2, Mo5
Awaous guamensis	O'opu nakea (N)	K6, K7
Bothus mancus	Flowery flounder (N)	Mo5
Caranx melampygus	Bluefin trevally (N)	Mo2
Chanos chanos	Milkfish (N)	H3, Mo2
Corydoras aeneus	**Bronze catfish (E)**	O5
Eleotris sandwicensis	Sandwich Island sleeper (End)	H2, H3, K1, K7, M5, O1, O13
Elops hawaiensis	Ladyfish (End)	K7, Mo2
Foa brachygramma	Bay cardinal fish (N)	Mo5
Gambusia affinis	**Mosquitofish (E)**	H1, H3, H6, K1, K2, K3, K4, K5, K8, M1, M2, M3, Mo1, Mo2, Mo3, Mo4, O2, O3, O4, O6, O7, O8, O10, O11
Hemichromis elongatus	**Banded jewel cichlid (E)**	O5, O13
Kuhlia sp.	Flagtail (End)	K7, M5, Mo1
Kuhlia xenura	Hawaiian flagtail (End)	Mo2, O13
Kuhlia sandvicensis	Zebra-head flagtail (End)	H3, Mo5
Limia vittata	**Cuban molly (E)**	O3
Misgurnus anguillicaudatus	**Weather loach (E)**	M3,
Mugil cephalus	Striped mullet (N)	H2, H3, K7, M6, Mo1, Mo2, Mo5, O13
Mugilogobius cavifrons	**Mangrove goby (E)**	K7, Mo2, O4, O8, O9
Mulloidichthys vanicolensis	Yellowfin goatfish (N)	H2
Oreochromis mossambicus	**Mozambique tilapia (E)**	H1, H6, K3, K7, M1, Mo2, Mo4, O10, O11, O13
Poecilia spp.	**Liberty/Mexican molly (E)**	H2, H5, H6, K2, K3, K4, K5, K7, K8, M1, M2, M6, Mo1, Mo2, Mo3, Mo4, Mo5, O2, O3, O4, O5, O6, O7, O8, O9, O10, O11, O13
Poecilia latipinna	**Sailfin molly (E)**	O3
Poecilia reticulata	**Guppy (E)**	H1, K1, K3, K7, Mo3,
Polydactylus sexfilis	Pacific threadfin (N)	H3
Psilogobius mainlandi	Hawaiian shrimp goby (End)	H2, H3
Spratelloides delicatulus	**Blue sprat (E)**	O9
Stenogobius hawaiiensis	O'opu naniha (End)	H2, K2, K7, M6, O13
Sarotherodon melanotheron	**Black chin tilapia (E)**	K7, O10, O11

Table 2 (continued)

Taxa/scientific name	Common name	Sampling site
Saurida nebulosa	Nebulous lizardfish (N)	Mo5
Synodua variegatus	Reef lizardfish (N)	Mo5
Tilapia	**Various tilapia species (E)**	H6, K2, K3, K4, K7, M1, M2, Mo1, Mo2, Mo4, O2, O3, O4, O6, O7, O8, O9, O10, O11, O12, O13
Tilapia zillii	**Redbelly tilapia (E)**	M1, O11
Valamugil engeli	**Australian mullet (E)**	H2, H3, K7, Mo2, Mo5
Xiphophorus helleri	**Swordtail (E)**	H6, K1, K5
Amphibians		
Bufo marinus	**Cane toad (E)**	K8, O8, O13
Rana catesbeiana	**Bullfrog (E)**	K1, K5

See Table 1 for specific wetland names. Bold names represent exotic (*E*) species collected, non-bold names represent native (*N*), and endemic (*End*) species

Oahu) nor wetland type (semi-natural, restored, created) was responsible for patterns of similarity. Instead, hydrological connection to the ocean was the most influential factor structuring nekton assemblages (Fig. 4). The community structure of nekton assemblages significantly differed across open, semi-open, and isolated wetlands (ANOSIM, $R=0.4$, $p<0.01$), which SIMPER analyses revealed were due to the higher densities of exotic species in isolated wetlands compared with semi-open or open wetlands. *G. affinus* and *Poecilia* spp. contributed to 50–70% of dissimilarity between isolated and open and isolated and semi-open wetlands, respectively. Native feeble shrimp, half-spotted goby (*Asterropteryx semipunctatus*), and mullet had higher densities in open wetlands compared with the

Fig. 2 Average percent contribution of individual species to densities of small-bodied nekton assemblages sampled using lift nets from 38 coastal wetlands across the five main Hawaiian Islands in phase I (March 2007). *White shaded areas* represent native species, while *gray* and *black shaded areas* represent exotic species. Only juvenile tilapia were collected, which could not be positively identified to species in the field and were thus grouped under "Tilapia". *n* number of wetlands sampled on that island

isolated ones and contributed to 26% of dissimilarity between these different hydrological types.

A total of 4,116 nekton were sampled using throw nets and seines from December 2008 through June 2009 in phase II. Total numbers of nekton were higher for exotic species (3,427) than native species (689), while species richness was higher for native species (23) than exotic species (14). Five of the native species collected were endemic (*Abudefduf abdominalis*, *E. sandwicensis*, *Elops hawaiensis*, *K. sandvicensis*, *K. xenura*).

Examination of the large-bodied nekton assemblages sampled from the same 20 wetlands from December 2008 thru June 2009 revealed similar patterns observed from lift nets (Fig. 5), with the exceptions that the densities of large-bodied nekton were much lower than the small-bodied nekton and species richness was much higher for seine and throw net samples. Large-bodied nekton assemblages in 17 of the 20 wetlands were dominated by exotic fish, which was again due to high densities of mosquitofish, mollies, and tilapia. The increased numbers of tilapia at most sites were likely a result of change in gear type (i.e., large mesh seines and throw nets) used to sample fish. Unfortunately, the presence of exotic tilapia in the Aimakapa wetland on Hawaii Island was a new record. Exotic tilapia were largely represented by the Mozambique (*Oreochromis mossambicus*) and black chin (*Sarotherodon melanotheron*). Another observation made during this study was the increased numbers of exotic *Poecilia* spp. in the Honuapo wetland on Hawaii Island (Figs. 3, 5), which was dominated by native species when sampling began in March 2007.

Densities of native large-bodied nekton species were only dominant in three of the 20 wetlands [Kaloko (Hawaii), Koheo (Molokai), Ualaupue (Molokai)]. Native species were represented by mullet, flagtails, and feeble
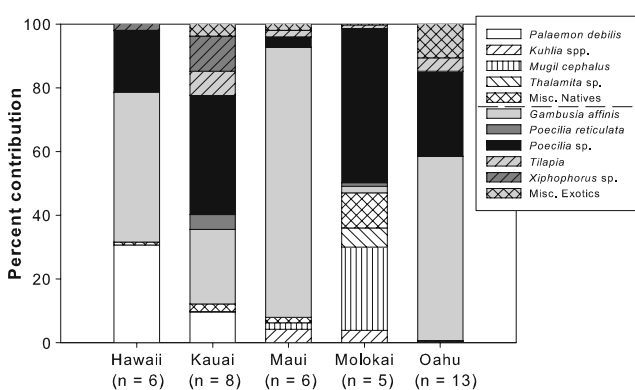
Fig. 3 Seasonal densities (numbers per square meter) of small-bodied nekton species sampled using lift nets from each of the 20 coastal wetlands across the five main Hawaiian Islands in phase II (September 2007–September 2008). *White shaded areas* represent native species, while *gray* and *black shaded areas* represent exotic species. Only juvenile tilapia were collected, which could not be positively identified to species in the field and were thus grouped under "Tilapia." Nekton were never observed or sampled from Nuu or Waihee, but were present in Kawainui and could not be captured
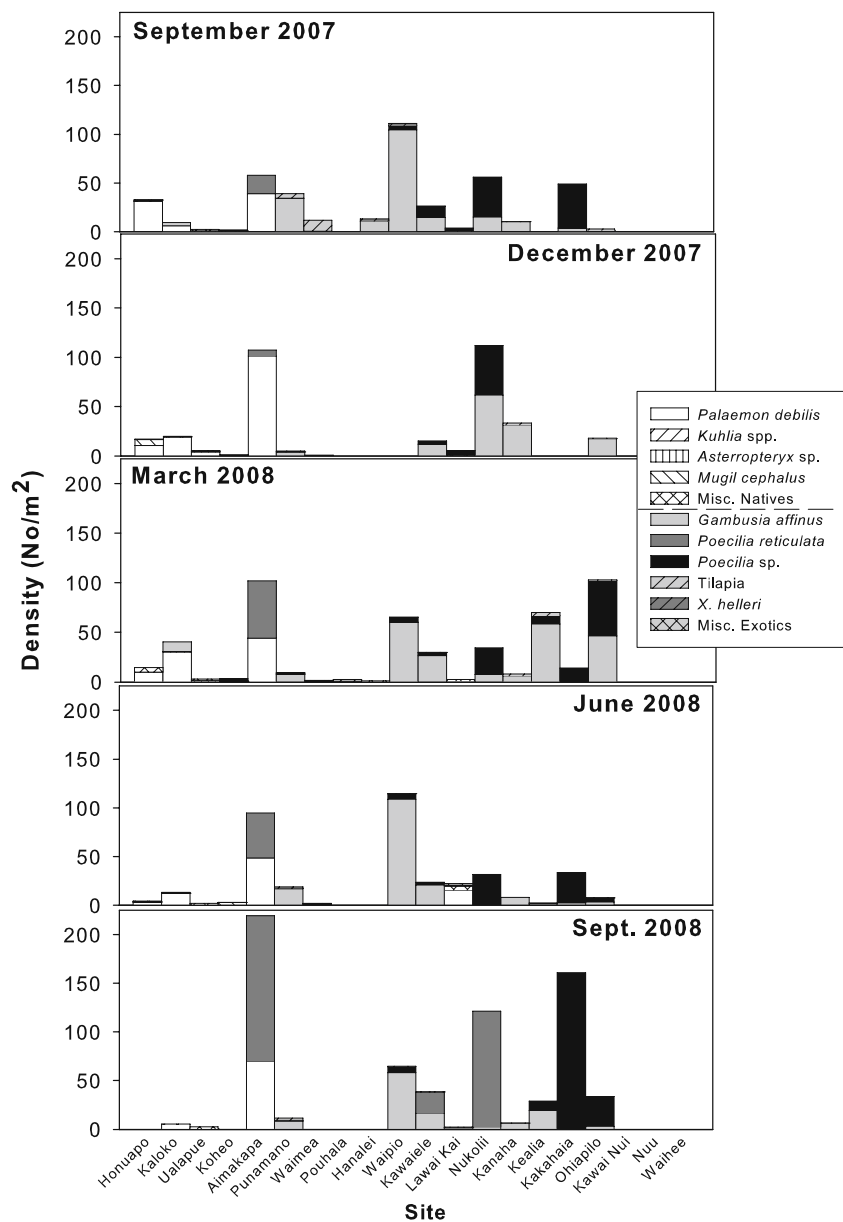
shrimp; less abundant native species included the predatory jack (*Caranx melampygus*).

Relationship Between Exotic Fish Density and Native Species Richness

Results from Honuapo seine and throw net datasets were considered to be an outlier in our linear regression analyses as this system, which was previously dominated by native species (March 2007 to December 2008), was dominated by *Poecilia* spp. by the end of our sampling efforts (June 2008). Thus, these data from Honuapo were not included in the regression analysis of the seine and throw net data.
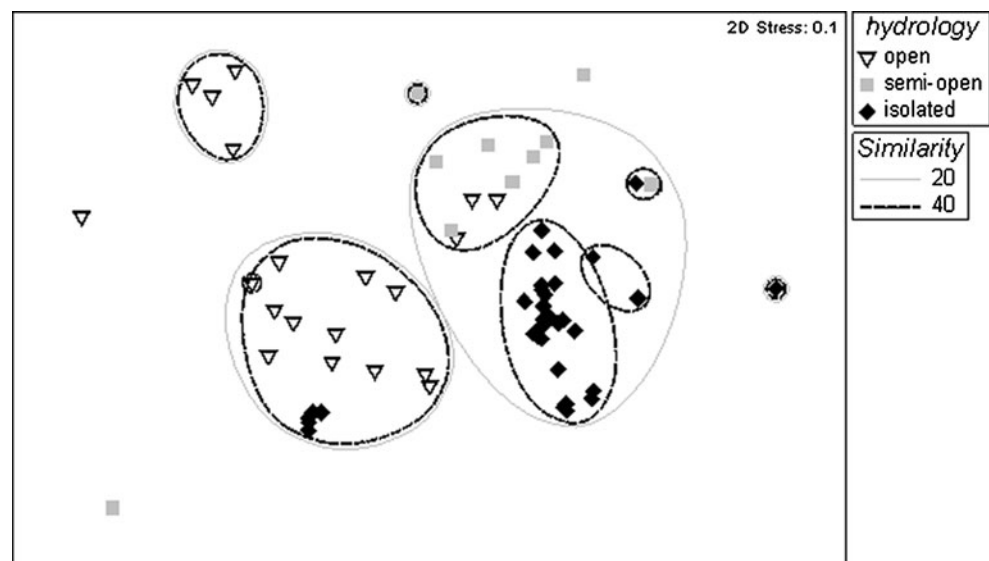
Exotic fish densities significantly decreased with increasing species richness for both lift nets ($r^2 = 0.50$,

$p < 0.001$) and seines and throw nets ($r^2 = 0.27$, $p < 0.05$; Fig. 6). Higher densities of exotic fish were observed in lift net samples from wetlands with one or fewer native species present and then decreased by 38–57% with every additional native species. Similarly, higher densities of exotic fish were observed in seines and throw net samples from wetlands with two or fewer native species present. Exotic fish densities decreased by 11–30% with every additional native species.

Relationship Between Nekton Densities and Environmental Variables

The combination of four environmental variables (salinity, pH, DO, temperature) provided the best correlation with

Fig. 4 NMDS of nekton densities from lift net samples collected throughout phase II. Hydrological connection to the ocean clustered data into four groups at the 40% similarity level

nekton community structure. However, this pattern was not significant ($\rho = 0.18$, $p > 0.05$). Pearson's correlations revealed that densities of mosquitofish, mollies, and total densities of exotic fish were significantly and positively correlated to the concentrations of TDN and temperature (Table 3). Densities of mosquitofish were also significantly and positively correlated to TP. There were no significant correlations between nekton densities and other physicochemical parameters such as temperature, depth, salinity, or dissolved oxygen.

Discussion

Nekton communities from Hawaiian coastal wetlands were generally dominated by exotic fish species, mainly poeciliids and tilapia. Native species were also present, but at densities much lower than exotics and were only dominant in a few wetland ecosystems. Hydrological connection to the ocean proved to be more important in structuring nekton communities than wetland type (semi-natural, created, restored), island, or other physicochemical parameters measured (e.g., water depth, dissolved oxygen, temperature). Exotic nekton were prevalent in closed/hydrologically isolated ecosystems, although high densities of exotic nekton were occasionally observed in semi-open and open wetlands as well. Native species were typically found in open and semi-open wetlands (Fig. 7). Isolated wetlands are a natural component of Hawaiian wetlands (Erickson and Puttock 2006; Bantilan-Smith et al. 2009), but provide habitat for only a few species of endemic, small-bodied (<2 cm) atyid shrimp, alpheid shrimp, and gobiid fish, although larger reef species can also be present (e.g., *Acanthurus triostegus*; Maciolek 1983; 1986). Higher densities of exotic versus native nekton in isolated wetlands

may have resulted from exotic species outcompeting and eventually eliminating these native populations, especially as native nekton in isolated wetlands typically exhibit lower densities or disappear completely with the introduction of exotic fish (Brock 1995; Hamer et al. 2002; Leyse et al. 2004; Ayala et al. 2007; Pyke 2008; Capps et al. 2009). Alternatively, higher densities of exotic nekton in isolated wetlands may have been due to the invasion of wetlands devoid of native nekton. Poeciliids and tilapia can tolerate the elevated salinities, elevated temperatures, and depleted dissolved oxygen levels that were often observed in isolated wetlands and were attributed to the evaporation of water (Bantilan-Smith et al. 2009). Long-term exposure to these same conditions can be lethal for native species (e.g., *E. sandwicensis*, *S. hawaiiensis*) that prefer cooler, higher oxygenated waters (Hathaway 1978; Yamamoto and Tagawa 2000). Semi-open wetlands periodically had elevated salinities, elevated temperatures, and depleted dissolved oxygen levels as well. However, native species could tolerate these conditions as reconnection to the ocean via high spring tides or storm surges replenished these ecosystem with cooler, less saline ocean water (Bantilan-Smith et al. 2009; Fig. 7).

Higher densities and species richness of native species in open and semi-open wetlands (Fig. 7) were due to transient, nearshore fish species (e.g., mullet, flagtails) utilizing coastal wetlands for feeding or nursery habitat (Erickson and Puttock 2006; MacKenzie, unpublished data). Connection to the ocean also allowed regular access by larger predatory fish such as jacks and barracuda that may have lowered exotic fish densities through predation (T. Sakihara, Hawaii Division of Aquatic Resources, personal communication; R. MacKenzie, unpublished data). These patterns, coupled with the negative relationship between exotic fish densities and native species richness, suggest that native biodiversity may

Fig. 5 Seasonal densities (numbers per square meter) of large-bodied nekton species sampled using seines and throw nets from each of the 20 coastal wetlands across the five main Hawaiian Islands in phase II (December 2008–June 2009). *White shaded areas* represent native species, while *gray* and *black shaded areas* represent exotic species. Identification of tilapia in the field was complicated by hybridization between species. Thus, tilapia are grouped under "Tilapia". Nekton were never observed or sampled from Nuu or Waihee
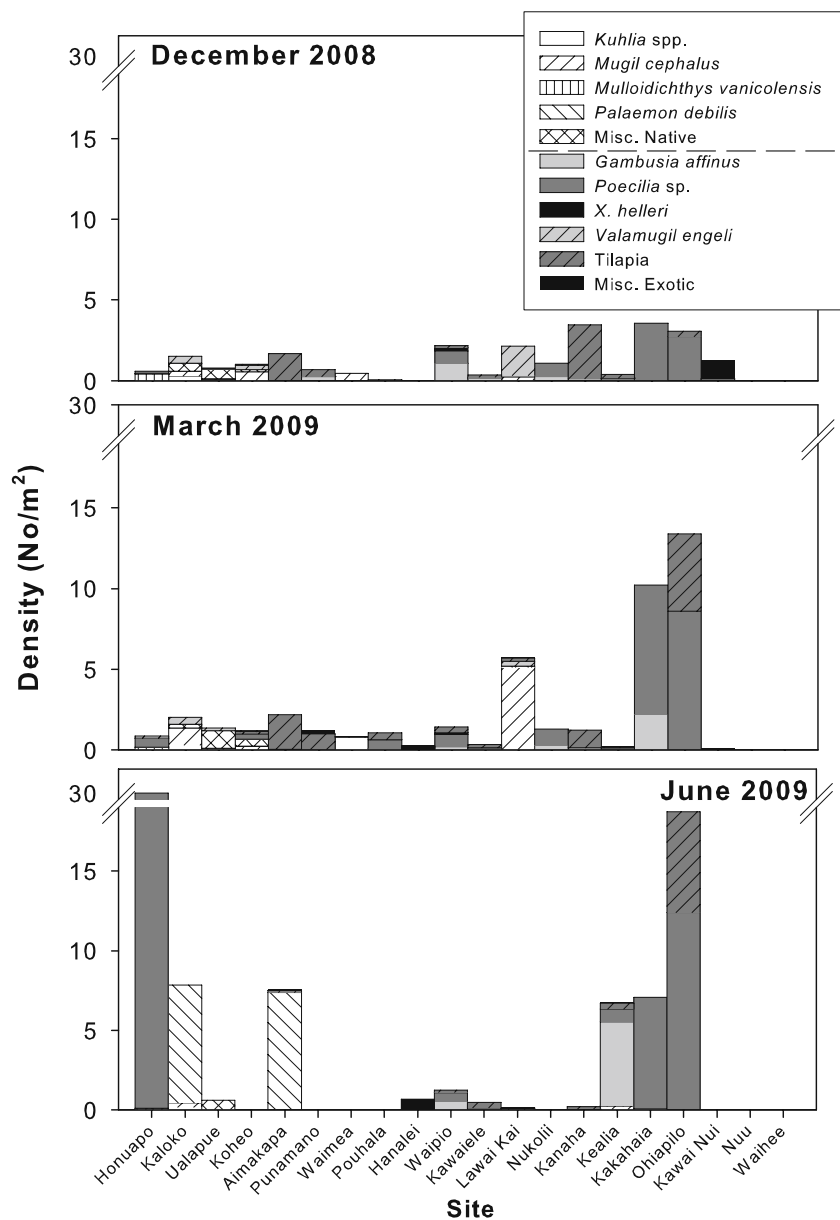
increase invasion resistance of coastal wetlands. While invasion resistance has been identified in other aquatic (Mitchell and Knouft 2009) and terrestrial studies (Levine and D' Antonio 1999; Boelman et al. 2007; Flaspohler et al. 2010), the negative relationship between exotic and native fish observed here could also be a result of exotic fish colonizing habitat unsuitable for native species, as discussed above. Additional robust experimental designs are needed to further explore this idea in coastal wetlands.

Spread, Establishment, and Abundance of Exotic Fish in Hawaii

The wide distribution of exotic fish species in coastal wetlands throughout the Hawaiian Islands was largely due to human introductions of those species. Many species of poeciliids have been and continue to be released to aquatic ecosystems for mosquito control or as unwanted aquarium pets (Nakagawa 1964; Yamamoto and Tagawa 2000; Englund 2002). Many tilapia species were introduced as potential aquaculture species and continue to be introduced to wetlands as a food resource for humans (Yamamoto and Tagawa 2000).

Physiological tolerance to a wide range of water temperatures, dissolved oxygen concentrations, and salinities is a trait that also allows exotic species to successfully establish populations in novel ecosystems (Moyle and Light 1996). Poeciliid and tilapia were often the only nekton collected from hypoxic (DO=2–4 mg/L, i.e., Nukolii, Kauai) or hyperhaline coastal wetlands (salinities>60‰, i.e., Pouhala,
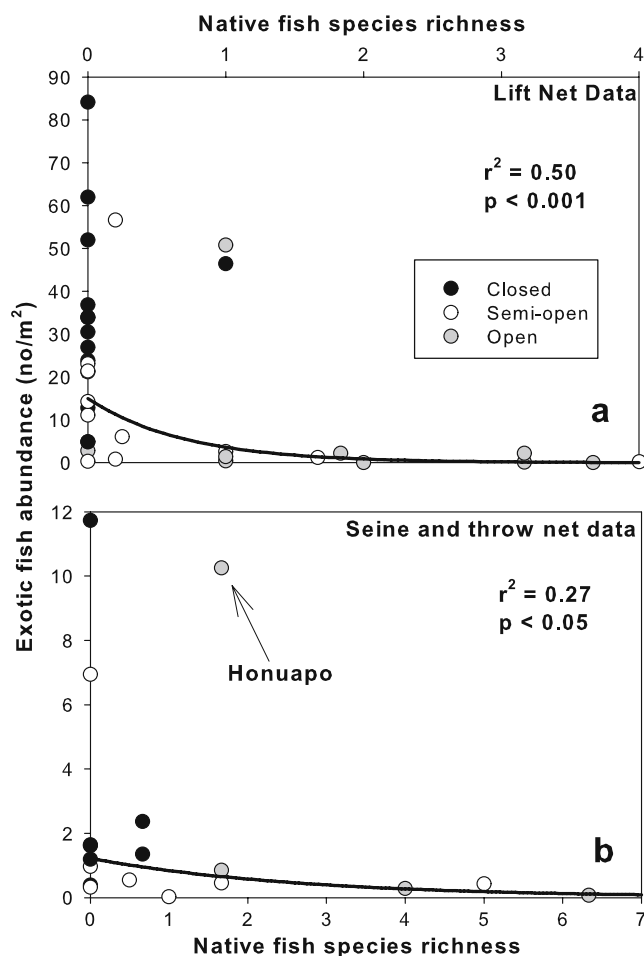
Fig. 6 Monthly averages (±1 SE) of exotic fish densities as a function of monthly averages (±1 SE) of native species richness in closed (*black circle*), semi-open (*white circle*), and open (*gray circles*) coastal wetlands sampled using lift net (**a**) and seine and throw net samples (**b**). Honuapo was considered to be an outlier to our seine and lift net data because exotic fish had only recently established a large population in this ecosystem. Therefore, it was not included in the linear analysis of this dataset

Table 3 Results from Pearson's correlations among exotic fish densities sampled using lift nets and nutrient measurements from all wetlands sampled from March 2007 through September 2008

Taxa	Factor	R	p
Gambusia affinis	TDN	0.25	0.05
	TP	0.21	0.05
	Salinity	−0.36	0.001
	Temperature	0.24	0.05
Poecilia spp.	TDN	0.28	0.01
	Temp.	0.32	0.001
Total exotic fish	TDN	0.30	0.01
	Temperature	0.26	0.05

TDN total dissolved nitrogen, *TP* total phosphorous, *Temperature* water temperature

Oahu; Table 1). This suggests that the physiological tolerance of these fish may be another factor involved in the establishment of poeciliid and tilapia populations in coastal wetlands across the Hawaiian Islands and that the ocean may provide a conduit between native and invaded ecosystems.

The reproductive traits of poeciliids and tilapia have also allowed them to successfully establish populations in Hawaiian ecosystems. Poeciliids give birth to live young fish (Meffe and Snelson 1989), while the two dominant tilapia species collected (*O. mossambicus* and *S. melano- theron*) are mouth brooders. These parental care strategies increase the survival of young, reduce their dispersal into poor habitat, and provide abundant populations to establish in new ecosystems (Marchetti et al. 2004a; Moyle and Marchetti 2006). The ability of both poeciliids and tilapia to spawn throughout the year in Hawaiian coastal wetlands (McGuire 2007; MacKenzie, unpublished data) also increases their ability to rapidly establish populations in novel ecosystems (Marchetti et al. 2004b; Moyle and Marchetti 2006).

The trophic status of poeciliids and tilapia was another factor that helped these exotic fish successfully establish populations throughout the Hawaiian Islands. The poeci- liids and tilapia collected are well-known omnivores (Harrington and Harrington 1982; Trewavas 1983; Bhakta and Bandyopadhyay 2007), which was confirmed by the gut content analysis of specimens collected from this study (R. MacKenzie, unpublished data). Because omnivores feed on a diversity of resources, there are unlimited supplies of food during the early stages of invasion as well as during the establishment of exotic fish populations (Moyle and Light 1996; Marchetti et al. 2004b).

Exotic Fish as Indicators of Coastal Wetland Habitat Quality

Native nekton assemblages have been used in other ecosys- tems as effective indicators of habitat quality (Karr 1981; Dionne 2000). It is possible that exotic nekton assemblages may potentially serve a similar purpose in the coastal wetlands of Hawaii. Differences in the tolerance thresholds of environmental parameters between native and exotic fish species discussed above suggest that the presence of high densities of exotic fish in coastal wetlands, especially in semi- open and open ones, may indicate poor habitat for native species and a degraded ecosystem. For example, the positive and significant correlations between exotic fish densities, temperature, and nutrients reported here suggest that the presence of high densities of exotic fish may indicate that water quality is impaired. Other studies have used exotic fish to monitor water quality of aquatic ecosystems (Crumby et al. 1990; Minns et al. 1994; Moyle and Randall 1998; Kennard

Fig. 7 Relationships between native species, exotic species, hydrological connection to the ocean, water depth, and salinity. Fish assemblages with high densities of native species and low densities of exotics in an open wetland (Ualapue) (**a**), fish assemblages with a mixture of exotic and native species in a semi-open wetland (Koheo) (**b**), and fish assemblages with high densities of exotic species in an isolated wetland (Ohiapilo) (**c**). *Dashed line* represents gear type which was changed from lift nets to seines and throw nets
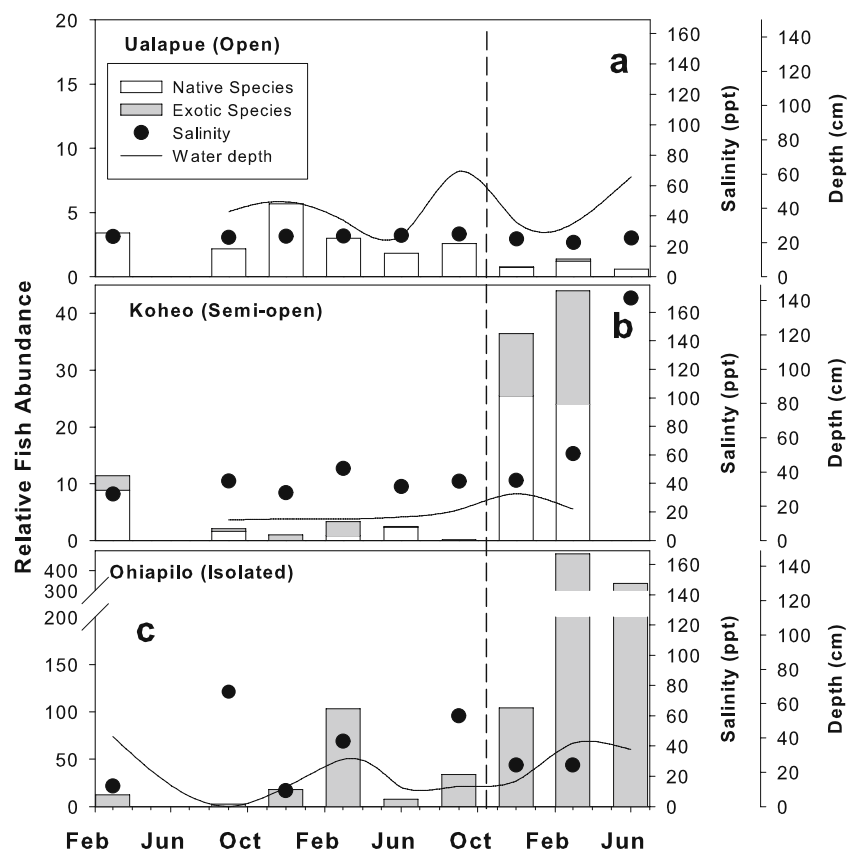
et al. 2005), but it is unclear whether exotic fish are an indicator or the cause of poor water quality (Kennard et al. 2005). For example, the correlation between exotic fish densities and TDN observed in this study may have been due to the wide range of physiological tolerances of poeciliids and tilapia. Alternatively, high densities of exotic fish may have been the source of elevated nutrients. The omnivorous nature of exotic fish sampled in Hawaii suggests that sediments and detritus are an important component of their diets. As a result, refractory nutrients bound up as organic matter are released to the water column in more labile, readily available forms that can be used by bacteria and other microorganisms and potentially lead to the eutrophication of coastal areas. A preliminary experimental nutrient flux study revealed that exotic fish excreted 15 times more TDN than native fish (R. MacKenzie, unpublished data). Future studies are needed to further examine the relationship between exotic fish and water quality parameters in Hawaiian coastal wetlands.

High densities of exotic fish may also support high densities of exotic parasites. Exotic parasites arrived with the introduction of exotic fish and now heavily infest native fish, lowering their overall fitness and reproductive output (Font 2007). Most parasite studies have focused on native Hawaiian stream fauna (Font 1998, 2003, 2007), but parasites were observed on native fish at several of our coastal wetland sites (e.g., Lawai Kai, Kauai).

High densities of exotic fish in coastal wetlands also suggest that fewer food resources are available for native species. The exclusion of exotic fish from areas within a coastal wetland on the island of Oahu increased insect emergence as well as stem densities of the aquatic macrophyte *Ruppia maritima*, important food sources for the endangered Hawaiian moorhen (*G. c. sandvicensis*; McGuire 2007). Exclosures in other island wetlands have had similar results (Mayer et al. 2008; K. Peyton, University of Hawaii Manoa, personal communication).

Conclusions

Exotic fish were well established in wetlands across the Hawaiian Islands, with densities up to 15 times greater than native species when natives were present. Wetlands with native-dominated nekton communities tended to have lower densities of exotic fish. However, it was not clear whether this relationship was a function of native species richness, exotic fish densities, hydrological connection to the ocean, or other abiotic characteristics of invaded wetlands. The fact that very few wetlands sampled during this study were dominated by native nekton communities underscores the need to preserve these rare ecosystems, especially as native biodiversity may increase their resistance to invasion by

exotic nekton species. Continued monitoring of coastal wetlands is an important first step in the preservation of these native wetlands as it can detect the arrival of exotic species and help prevent them from successfully establishing populations.

Correlations among exotic fish densities and various water quality parameters suggest that exotic fish may function as indicators for habitat quality of Hawaiian coastal wetlands. Thus, the prevalence of poeciliids and tilapia in wetlands across the main Hawaiian Islands suggests that the habitat value of these ecosystems for native species may be highly impaired from hydrological alterations, increased nutrient inputs, or simply the presence of high densities of exotic fish. Future wetland restoration projects should include the eradication or control of exotic fish, which may be accomplished by maintaining hydrological connections between the ocean and wetland ecosystems.

References

ASTM. 1995. Annual Books of ASTM Standards, Section 11, Water and Environmental Technology, Volume 11.02, Water (I).

Allen, J.A., K.C. Ewel, B.D. Keeland, T. Tara, and T.J. Smith III. 2000. Downed wood in Micronesian mangrove forests. *Wetlands* 20: 169–176.

Ayala, J.R., R.B. Rader, M.C. Belk, and G.B. Schaalje. 2007. Ground-truthing the impact of invasive species: Spatio-temporal overlap between native least chub and introduced western mosquitofish. *Biological Invasions* 9: 857–869.

Balick, M.J. (ed.). 2009. *Ethnobotany of Pohnpei: Plants, people, and island culture*. New York City: New York Botanical Garden/University of Hawaii Press.

Bantilan-Smith, M., G.L. Bruland, R.A. MacKenzie, A. Henry, and C.R. Ryder. 2009. A quantitative assessment of the vegetation and soils of coastal lowland wetlands in Hawai`i. *Wetlands* 29: 1023–1036.

Bhakta, J.N., and P.K. Bandyopadhyay. 2007. Exotic fish biodiversity in Churni River of West Bengal, India. *Electronic Journal of Biology* 3: 13–17.

Boelman, N.T., G.P. Asner, P.J. Hart, and R.E. Martin. 2007. Multi-trophic invasion resistance in Hawaii: Bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications* 17: 2137–2144.

Brasher, A.M.D., C.D. Luton, S.L. Goodbred, and R.H. Wolff. 2006. Invasion patterns along elevation and urbanization gradients in Hawaiian streams. *Transactions of the American Fisheries Society* 135: 1109–1129.

Brock, R. E. 1995. Anchialine pool joint venture with the U.S. Fish and Wildlife Service and Huehue Ranch Associates, L. P. for the removal of exotic fishes from the trial pond complex at Kuki`o, North Kona, HI. Honolulu, Hawaii. 24 pp.

Capps, K.A., C.B. Turner, M.T. Booth, D.L. Lombardozzi, S.H. McArt, D. Chai, G. Nelson, and N.G.J. Hairston. 2009. Behavioral responses of the endemic shrimp *Halocaridina rubra* (Malacostraca: Atyidae) to an introduced fish, *Gambusia affinus* (Actinopterygii: Poeciliidae) and implications for the trophic structure of Hawaiian anchialine ponds. *Pacific Science* 63: 27–37.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional climate projections. In *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, 847–940. UK: Cambridge University Press.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.

Crumby, W.D., M.A. Webb, and F.K. Bulow. 1990. Changes in biotic integrity of a river in North-Central Tennessee. *Transactions of the American Fisheries Society* 119: 885–893.

Dahl, T. E. 1990. Wetland losses in the United States 1780's to 1980's. USGS. http://www.npwrc.usgs.gov/resource/wetlands/wetloss/index.htm. Accessed 10 June 2011.

DesRochers, D.W., S.R. McWilliams, M.D. Silbernagle, and J.M. Reed. 2009. Macronutrients profiles of wetland plants consumed by the Hawaiian Moorhen (*Gallinula chlorpus sandvicensis*). *Wetlands* 29: 845–853.

Dionne, M., 2000. Ecosystem indicator: nekton. In *Regional standards to identify and evaluate tidal wetland restoration in the Gulf of Maine*, eds. H. A. Neckles and M. Dionne, 7–9. Wells, ME: Wells National Estuarine Research Reserve Technical Report.

Drew, W.M., K.C. Ewel, R.L. Naylor, and A. Sigrah. 2005. A tropical freshwater wetland: III. Direct use values and other good and services. *Wetlands Ecology and Management* 13: 685–693.

Driver, L.J., G.L. Adams, and S.R. Adams. 2009. Fish assemblage of a cypress wetland within an urban landscape. *Southeastern Naturalist* 8: 527–536.

EPA. 2002. National wetlands mitigation plan. http://water.epa.gov/lawsregs/guidance/wetlands/upload/2003_07_10_wetlands_map1226withsign.pdf. Accessed 10 June 2010.

Eberhardt, A.L. 2004. Fish versus human corridors: The impacts of road culverts on nekton community composition and movement in New England salt marshes. MS thesis, University of New Hampshire, Durham, NH, 146 pp.

Elton, C.S. 1958. *The ecology of invasions by animals and plants*. London: Methuen.

Englund, R.A. 2002. The loss of native biodiversity and continuing nonindigenous species introductions in freshwater, estuarine, and wetland communities of Pearl Harbor, Oahu, Hawaiian Islands. *Estuaries* 25: 418–430.

Erickson, T.A., and C.F. Puttock. 2006. *Hawaii wetland field guide*. Honolulu: Bess Press Books.

Fishman, M.J. 1993. Methods of analysis by the U.S. Geological Survey National Water Quality Laboratory—Determination of

inorganic and organic constituents in water and fluvial sediments. U.S. Geological Survey Open-File Report 93-125, 217 pp.

Flaspohler, D.J., C.P. Giardina, G.P. Asner, P.J. Hart, J. Price, C.K. Lyons, and X. Castaneda. 2010. Long-term effects on fragmentation and fragment properties on bird species richness in Hawaiian forests. *Biological Conservation* 143: 280–288.

Font, W.F. 1998. Parasites in paradise: Patterns of helminth distribution in Hawaiian stream fishes. *Journal of Helminthology* 72: 307–311.

Font, W.F. 2003. Global spread of parasites: What do Hawaiian streams tell us? *BioScience* 53: 1061–1067.

Font, W.F. 2007. Parasites of Hawaiian stream fishes: Sources and impacts. *Bishop Museum Bulletin in Cultural and Environmental Studies* 3: 157–169.

Grabarkiewicz, J. and W. Davis. 2008. An introduction to freshwater fishes as biological indicators. EPA-260-R-08-016, U.S. Environmental Protection Agency, Office of Environmental Information, Washington, DC, 96 pp.

Hamer, A.J., S.J. Lane, and M.J. Mahony. 2002. The role of introduced mosquitofish (*Gambusia holbrooki*) in excluding the native green and golden bell frog (*Litoria aurea*) from original habitats in south-eastern Australia. *Oecologia* 132: 445–452.

Harrington, R.W.J., and E.S. Harrington. 1982. Effects on fishes and their forage organisms of impounding a Florida salt marsh to prevent breeding by salt marsh mosquitoes. *Bulletin of Marine Science* 32: 523–531.

Hathaway, C.B. 1978. Stream channel modification in Hawaii. Part C: Tolerance of native stream species to observed levels of environmental variability. USFWS National Stream Alteration Team, FWS/OBS-78/18, Columbia, Missouri, 59 pp.

Holitzki, T. 2010. Impacts of invasive poeciliid fish on Hawaiian stream ecosystems. MS thesis, University of Hawaii at Hilo, Hilo, HI, 51 pp.

Karr, J.R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* 6: 21–27.

Kennard, M.J., A.H. Arthington, B.J. Pusey, and B.D. Harch. 2005. Are alien fish a reliable indicator of river health? *Freshwater Biology* 50: 174–193.

Kosaka, E. 1990. Technical review of draft report, wetlands losses in the United States, 1780's to 1980's. Washington DC, USA, 3 pp.

Levine, J.M., and C.M. D' Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87: 15–26.

Leyse, K.E., S.P. Lawler, and T. Strange. 2004. Effects of an alien fish, *Gambusia affinis*, on an endemic California fairy shrimp, *Linderiella occidentalis*: Implications for conservation of diversity in fishless waters. *Biological Conservation* 118: 57–65.

Maciolek, J.A. 1983. Distribution and biology of Indo-Pacific insular hypogeal shrimps. *Bulletin of Marine Science* 33: 606–618.

Maciolek, J.A. 1986. Environmental features and biota of anchialine pools on Cape Kinau, Maui, Hawaii. *Stygologia* 2: 119–129.

MacKenzie, R.A., and M. Dionne. 2008. Habitat heterogeneity: The importance of salt marsh pools and high marsh surfaces to fish production in two Gulf of Maine salt marshes. *Marine Ecology Progress Series* 368: 217–230.

Marchetti, M.P., P.B. Moyle, and R. Levine. 2004a. Alien fishes in California watersheds: Characteristics of successful and failed invasions. *Ecological Applications* 14: 587–596.

Marchetti, M.P., P.B. Moyle, and R. Levine. 2004b. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49: 646–661.

Mayer, T., M. Nishimoto and G. Nakai. 2008. The relationship between midge, fish, and abiotic factors at Kealia Pond NWR. 20 pp.

McGuire, C. R. 2007. Effects of introduced fish on aquatic insect abundance: A case study of Hamakua marsh, Oahu, Hawaii. MS, University of Hawaii at Manoa, Honolulu, HI, 116 pp.

Meffe, G.K., and F.F. Snelson. 1989. An ecological overview of poeciliid fishes. In *Ecology and evolution of livebearing fishes (Poeciliidae)*, ed. G.K. Meffe and F.F. Snelson Jr., 13–31. New Jersey: Prentice Hall.

Minns, C.K., V.W. Cairns, R.G. Randall, and J.E. Moore. 1994. An index of biotic integrity (IBI) for fish assemblages in the littoral zone of Great Lakes' areas of concern. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1804–1822.

Mitchell, A.L., and J.H. Knouft. 2009. Non-native fishes and native species diversity in freshwater fish assemblages across the United States. *Biological Invasions* 11: 1441–1450.

Moyle, P.B., and T. Light. 1996. Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation* 78: 149–161.

Moyle, P.B., and M.P. Marchetti. 2006. Predicting invasion success: Freshwater fishes in California as a model. *BioScience* 56: 515–524.

Moyle, P.B., and P.J. Randall. 1998. Evaluating the biotic integrity of watersheds in the Sierra Nevada, California. *Conservation Biology* 12: 1318–1326.

Nakagawa, P.Y. 1964. Mosquito control in Hawaii. *Pest Control Magazine* 32: 1–3.

Nakahara, B. A., 2007. Utilization of mangrove habitat by megafauna along the southern coast of Molokai, Hawaii. Master's thesis, University of Hawaii at Manoa, Honolulu, 86 pp.

Naylor, R., and M. Drew. 1998. Valuing mangrove resources in Kosrae, Micronesia. *Environment and Development Economics* 3: 471–490.

Patton, C.J. and J.R. Kryskalla. 2003. Methods of analysis by the U.S. Geological Survey National Water Quality Laboratory—Evaluation of alkaline persulfate digestion as an alternative to Kjeldahl digestion for determination of total dissolved nitrogen and phosphorus in water. U.S. Geological Survey Water Resources Investigations Report 03-4174, 40 pp.

Paulay, G. 1994. Biodiversity on oceanic islands: Its origin and extinction. *American Zoologist* 34: 134–144.

Pyke, G.H. 2008. Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. *Annual Review of Ecology and Systematics* 39: 171–191.

Reed, J.M., M.D. Silbernagle, K. Evans, A. Engilis Jr., and L.W. Oring. 1998. Subadult movement patterns of the endangered Hawaiian stilt (*Himantopus mexicanus knudseni*). *Auk* 115: 791–797.

Roman, C.T., K.B. Raposa, S.C. Adamowicz, M.J. James-Pirri, and J. G. Catena. 2002. Quantifying vegetation and nekton response to tidal restoration of a New England salt marsh. *Restoration Ecology* 110: 450–460.

Scott, D.A. 1993. *A directory of wetlands in Oceania*. Slimbridge, UK: International Waterfowl and Wetlands Research Bureau.

Seilheimer, T.S., and P. Chow-Fraser. 2007. Application of the wetland fish index to northern Great Lakes marshes with emphasis on Georgian Bay coastal wetlands. *Journal of Great Lakes Research* 33: 154–171.

Trewavas, E. 1983. *Tilapine fishes of the genera Sarotherodon, Oreochromis, and Danakilia*. Ithaca: Cornell University Press.

USEPA. 1983. Determination of nitrate and nitrite in estuarine and coastal waters by gas segmented continuous flow, colorimentric analysis. In *Methods for chemical analysis of water and wastes*, EPA-600/4 4-79-020 353-2.1-2.5. Cincinnati, OH, USA.

Williams, G.D., and J.B. Zedler. 1999. Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: Relative influence of channel morphology and restoration history. *Estuaries* 22: 702–716.

Yamamoto, M.N., and A.W. Tagawa. 2000. *Hawaii's native and exotic freshwater animals*. Honolulu: Mutual Publishing.